

A latitudinal gradient in herbivore resistance in common sunflower, *Helianthus annuus* (Asteraceae)

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Background and aims – The intensity of herbivory is expected to decline with increasing latitude. As herbivory varies spatially and over time, a reliable method of assessing the intensity of herbivory is to examine the degree of herbivore resistance in the plant community. Latitudinal gradients in resistance to herbivory were examined in wild populations of common sunflower, *Helianthus annuus*.

Materials and methods – Seeds from 23 different latitudes, ranging from 20 to 44°N, were obtained from the USDA's Germplasm Resources Information Network. Plants were grown in a greenhouse for nine weeks. At that time, the size (height, leaf length, number of leaves) and resistance of each plant to herbivory (determined through a bioassay using a generalist herbivore, *Helicoverpa zea*) was assessed.

Key results – Resistance to herbivory decreased significantly with latitude, while plant size, as indicated by height, was positively correlated with latitude and negatively correlated with both temperature and resistance to herbivory.

Conclusion – Populations from lower latitudes exhibited elevated resistance to herbivory and slower growth, suggesting first, that herbivory is more intense at lower latitudes and second, that there is a tradeoff between growth and defense.

Keywords – Common sunflower; *Helianthus annuus*; *Helicoverpa zea*, herbivory; latitudinal gradient; resistance; tradeoff.

INTRODUCTION

Examination of latitudinal gradients may allow better prediction of the effects of global climate change on biotic interactions. As northern communities warm, they may begin to display some of the characteristics of more southerly ecosystems. Of particular importance to agriculture, forestry, and native species are the effects of climate change on plant-insect interactions (Zvereva & Kozlov 2006). Because southern ecosystems do not experience seasonal disruptions in growth, they are expected to support a more diverse and abundant community of herbivores, leading to more intense herbivory at lower latitudes (Morriën et al. 2010; Moles et al. 2011). Although insect diversity does tend to decrease

with increasing latitude (Bale et al. 2002; Willig et al. 2003), studies of latitudinal gradients in the intensity of herbivory have had mixed results. Several studies have documented increased levels of herbivory at lower latitudes (Garibaldi et al. 2011; Zhang et al. 2011), but many have not (Andrew & Hughes 2005; Adams & Zhang 2009; Adams et al. 2009; Woods et al. 2012).

Examination of the intensity of herbivory over wide latitudinal gradients has proven methodologically challenging (Anstett et al. 2016; but see Lehndal & Ågren 2015). Herbivore activity varies widely from one year to the next and throughout the growing season, and is significantly impacted by weather, especially temperature and rainfall. Despite rigorous efforts to collect data, studies of this scale are fraught

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with problems related to the duration of data collection (any one year of data may not reflect average herbivore damage), timing of data collection (researchers may not be able to simultaneously collect data at many geographically distant sites), and assessment of damage (if a plant abscises tissue damaged by herbivores, it is not obvious that the plant has sustained injury). It is not surprising then that studies of latitudinal gradients have mixed results.

In contrast, the strength of a plant's resistance to herbivores is a product of its evolutionary history (Bidart-Bouzat & Imeh-Nathaniel 2008). As such, it is not as likely to reflect random events and weather patterns as much as climate and the intensity of herbivory over longer time frames. While even moderate levels of herbivore attack can have large impacts on plant fitness, investment in defense in the absence of herbivores would be costly. Plants that invest heavily in defense grow more slowly (Huot et al. 2014) and as a result have reduced total leaf area, which leads to lower levels of photosynthesis and, ultimately, even lower growth rates. The intensity of herbivore attack is a powerful selection pressure, dictating the degree to which plants are able to invest in growth as opposed to defense (Coley 1983; de Jong et al. 1995; Fine et al. 2006; Van Zandt 2007; Huot et al. 2014).

Plants from regions with lower intensities of herbivory should display reduced resistance compared to plants from regions with higher intensities of herbivory. The latitudinal-herbivory defense hypothesis (LHDH) predicts that plants from lower latitudes will express stronger herbivore defenses owing to the greater diversity and abundance of herbivores (Schemske et al. 2009; Kim 2014). However, as with the hypothesis that the intensity of herbivory will be higher at lower latitudes, LHDH has had mixed support. In fact, Moles et al. (2011) found only 37% of studies reported higher levels of herbivore defenses at lower latitudes and later suggested that LHDH could be a 'zombie' hypothesis (Moles & Ollerton 2016), continuing on long after sufficient evidence had accumulated to warrant its dismissal.

Plants have evolved a myriad of defensive strategies, including the production of secondary compounds that reduce their palatability to herbivores and/or slow herbivore growth rates, the production of volatile compounds used to attract predatory insects, and even the re-growth of lost tissues, which allows them to tolerate herbivore damage (Agrawal & Fishbein 2006). This complexity makes defensive strategies difficult to conceptualize, and yet many studies aiming to examine latitudinal gradients have evaluated specific chemical and physical traits that may or may not be related to resistance, e.g., tannin concentrations, leaf toughness, etc. (Moles et al 2011). These characteristics do not consistently predict the ability of plants to resist herbivory (Zvereva & Kozlov 2006; Carmona et al. 2011; Kim 2014). An effective demonstration of this problem is provided by a study conducted by Anstett et al. (2015), which described opposing trends in the latitudinal gradients of two related compounds (both ellagitannins) suspected of being important in the herbivore defenses of *Oenothera biennis* (though higher levels of all phenolic compounds were associated with lower latitudes). Direct observation of herbivore performance provides a more realistic portrait of plants defenses. Herbivores may not be responding to any one chemical or physical trait, but to

the entirety of the condition of the plant. By relying on bioassays, researchers are able to assess the totality of a plants' defenses (with the exception of indirect defenses) and avoid predicting which particular traits may be involved in herbivore resistance.

In this study, I examine the herbivore resistance and growth rates of *Helianthus annuus* L. (common sunflower) from 23 populations ranging from 20 to 44°N. *Helianthus annuus* spans an exceptionally wide latitudinal range and provides a unique opportunity to examine trends on a continental scale. Here, direct observation of herbivore performance is relied on to observe plant resistance. I ask the following questions: Does herbivore resistance of *H. annuus* to the generalist herbivore *Helicoverpa zea* (Boddie) vary with latitude? Does investment in growth of *H. annuus* vary with latitude? Is there a tradeoff between herbivore resistance and growth? Here I focus on the response of a generalist herbivore because they are predicted to be more successful than specialists in the face of rising temperatures owing to their ability to shift their ranges northward even in the absence of their food source (Berg et al. 2010).

MATERIAL AND METHODS

Study species

Helianthus annuus L., or wild or common sunflower, is an annual plant native to North America. It is found throughout the United States, Canada, and Mexico (Halvorson & Guertin 2003). Domesticated varieties are important agricultural crops, while many wild strains are important agricultural weeds. *Helianthus annuus* germinates in early spring and flowers from July to October. Each plant produces many yellow and brown composite flowers and can yield upwards of 7200 seeds (Stevens 1932; Halvorson & Guertin 2003). Heights are variable, but range from 0.3 to 2 m. Seeds used in this experiment were obtained from the USDA's Germplasm Resources Information Network. All accessions were listed as wild material. A list of accession numbers, collection coordinates, and site descriptions can be found in table 1. Seed collection dates ranged from the early 1970s to 1991, with most accessions collected from the field in the 1970s (table 1). Because temperatures increased in the subsequent decades, the mean temperature between 1981 and 2010 (table 1) may be slightly higher than those experienced by the ancestral plant populations. However, the latitudinal gradient in temperature change is not likely to have changed, with temperature increasing with decreasing latitude.

Helicoverpa zea (Boddie) (Lepidoptera: Noctuidae) or corn earworm, is a generalist herbivore that is known to attack *H. annuus*. Eggs were obtained from Benzon Research (Carlisle, Pennsylvania).

Helianthus annuus growth

The experiment was conducted in three separate temporal blocks, with approximately 1/3 of the 23 accessions included in each block. Each block contained accessions from throughout the latitudinal range. Plants were grown in square pots, 8.4 cm wide and 8.9 cm deep, filled with Metro-Mix

Table 1 – *Helianthus annuus* seed accessions provided by the USDA’s Germplasm Resources Information Network.

Accessions sorted by latitude. Climate data gathered from the National Oceanic and Atmospheric Administration. *Temperature is the average annual temperature from 1981–2010 recorded at the closest National Oceanic and Atmospheric Administration weather station. **Precipitation is the average annual precipitation from 1981–2010 recorded at the closest National Oceanic and Atmospheric Administration weather station. ***Collection sites located in Mexico. Temperature and precipitation data were estimated from the closest city reported by TuTiempo (continuously updated).

Accession #	Latitude	Longitude	Collection date	Average annual temperature* (°C)	Average annual precipitation** (mm)
PI 413066***	20°03'00"	-100°25'12"	pre-1974	18.40	477.42
PI 413069***	22°46'48"	-103°31'12"	pre-1974	18.37	265.60
PI 413125	22°47'24"	-103°31'12"	pre-1974	18.37	265.60
PI 468451	26°12'36"	-98°19'48"	1979	24.22	563.88
PI 435435	27°13'28"	-98°08'24"	1976	22.40	672.34
PI 468525	28°30'00"	-100°17'60"	1980	21.89	513.84
PI 468510	28°39'36"	-96°32'60"	1980	21.44	1076.71
PI 468526	28°46'48"	-100°30'36"	1980	21.89	518.41
PI 468509	28°51'36"	-95°56'24"	1980	21.39	1241.81
PI 435418	29°32'24"	-95°01'12"	1976	20.28	1442.97
PI 613732	32°44'24"	-114°37'48"	1979	24.39	90.42
PI 613733	33°01'48"	-115°25'12"	pre-1974	22.56	73.66
PI 413099	35°02'60"	-118°09'36"	pre-1974	17.06	169.42
PI 435612	35°43'48"	-81°20'24"	1977	14.89	1175.00
PI 613752	35°57'36"	-83°55'12"	1975	14.00	1319.02
PI 413100	36°31'48"	-120°05'60"	pre-1974	17.56	213.36
PI 413088	36°49'12"	-119°59'24"	pre-1974	16.72	794.00
PI 413139	38°32'24"	-121°44'24"	pre-1974	16.22	497.84
PI 413129	38°40'48"	-121°46'12"	pre-1974	17.11	542.04
PI 435540	41°31'12"	-88°04'12"	1976	10.33	934.97
PI 468438	43°04'12"	-89°24'00"	1979	8.17	946.66
PI 597893	43°40'48"	-97°22'48"	1982	7.33	686.05
PI 586884	44°01'12"	-97°09'00"	1991	6.94	655.32

360 growing medium. Nine pots of each of the 23 accessions were established (207 pots in total). Ten seeds of each accession were planted in each pot. Extra seedlings were removed as they germinated until one seedling remained in each pot. Plants were fertilized with 14-14-14 (nitrogen-phosphorus-potassium) slow release fertilizer and grown in a greenhouse under natural light. Plant size, as indicated by height and number and size of leaves, was recorded after nine weeks of growth. Leaf size was estimated by measuring the length of the longest leaf blade to the nearest mm.

Herbivory resistance

After nine weeks of growth, bioassays were conducted to examine resistance to herbivory. Herbivore performance,

or growth, was used as an indication of the degree of plant defense (Van Zandt 2007; Kempel et al. 2011, 2013). Caterpillars grow slowly on well defended plants and more rapidly on poorly defended plants. *Helicoverpa zea* eggs were hatched at room temperature. Newly hatched caterpillars were assumed to be approximately the same size at hatching making any differences in biomass due to the quality of plant material consumed. Shortly after hatching, caterpillars were placed singly in 5.5 cm Petri dishes lined with filter paper moistened with de-ionized water. One or two young leaves from each of the nine plants from each of the 23 accessions were added individually to Petri dishes (again, the bioassays were necessarily completed in three temporal blocks, as described above). Being less well-defended than older leaves,

young leaves present a significant vulnerability of plants to herbivore attack. Because herbivores have been shown to prefer younger leaves (Coley 1980; Baskett & Schemske 2018), selection for increased investment in defense is most likely to be evident in newly formed leaves. The amount of leaf material provided was in excess of what the caterpillars could consume while in the dishes and in no case did the insects consume all of the leaf material provided. Dishes were sealed with Parafilm to prevent desiccation of the leaf material and caterpillar escape. After seven days, caterpillars were removed, placed in centrifuge tubes, and euthanized by freezing. They were then weighed (fresh mass) to the nearest thousandth of a milligram.

Average annual temperature and precipitation

The average annual temperature (degrees Celsius) and total annual precipitation (mm) of each accession collection site located in the United States was estimated from the averages reported between 1981 and 2010 of the closest National Oceanic and Atmospheric Administration weather station (National Oceanic and Atmospheric Administration 1981–2010). The average annual temperatures of the collection sites of the two genotypes collected in Mexico were estimated from the average annual temperatures of the closest city reported by TuTiempo (TuTiempo continuously updated).

Statistical analysis

Statistical analyses were conducted using SAS ver. 9.4 (SAS Institute Inc., Cary, North Carolina). Individual plants of each accession were not independent of each other. For this reason, analyses were conducted examining the mean size or mean caterpillar mass for each accession or genotype. Dead plants were not included in the calculation of mean plant sizes. Mass of *H. zea*, leaf length, number of leaves, and plant height were log transformed to reduce the positive skew in

the distributions. The effects of the block on the relationship between the three measures of plant size and the caterpillar size and latitude and temperature of the collection site was examined using generalized linear mixed-effects models (PROC GLM) with block included as a random-effects term. As there was no significant effect of the block in any of the six analyses, it was not included in the final analysis. Linear regressions were conducted to examine the relationships between the leaf length, number of leaves, and height of *H. annuus*, and the mass of *H. zea*, with temperature, precipitation, and latitude (PROC REG). Temperature and latitude were collinear so were considered separately.

The relationship between average annual temperature, average annual cumulative precipitation, latitude, and longitude was examined (PROC CORR). Temperature and precipitation were not correlated ($r = -0.2177$; $p = 0.3068$). Temperature was negatively correlated with latitude ($r = -0.8062$; $p < 0.0001$), but not correlated with longitude ($r = -0.2256$; $p = 0.2891$). Precipitation was not correlated with latitude ($r = 0.0942$; $p = 0.6613$) or temperature ($r = -0.2177$; $p = 0.3068$), but was correlated with longitude ($r = 0.6843$; $p = 0.0002$).

RESULTS

Caterpillar mass was positively related to latitude and negatively related to temperature, indicating stronger herbivore resistance at lower latitudes and higher temperatures (fig. 1). The linear regressions of log-caterpillar mass against latitude and temperature were highly significant ($r^2 = 0.1995$, model $F_{1,22} = 5.48$, $p = 0.0287$ and $r^2 = 0.2469$, model $F_{1,22} = 7.21$, $p = 0.0135$) (fig. 1). In contrast, log-caterpillar mass was unrelated to average cumulative precipitation ($r^2 = 0.0010$, model $F_{1,22} = 0.06$, $p = 0.8791$) (fig. 1).

The different measures of plant size displayed inconsistent relationships with latitude (fig. 2). While mean height

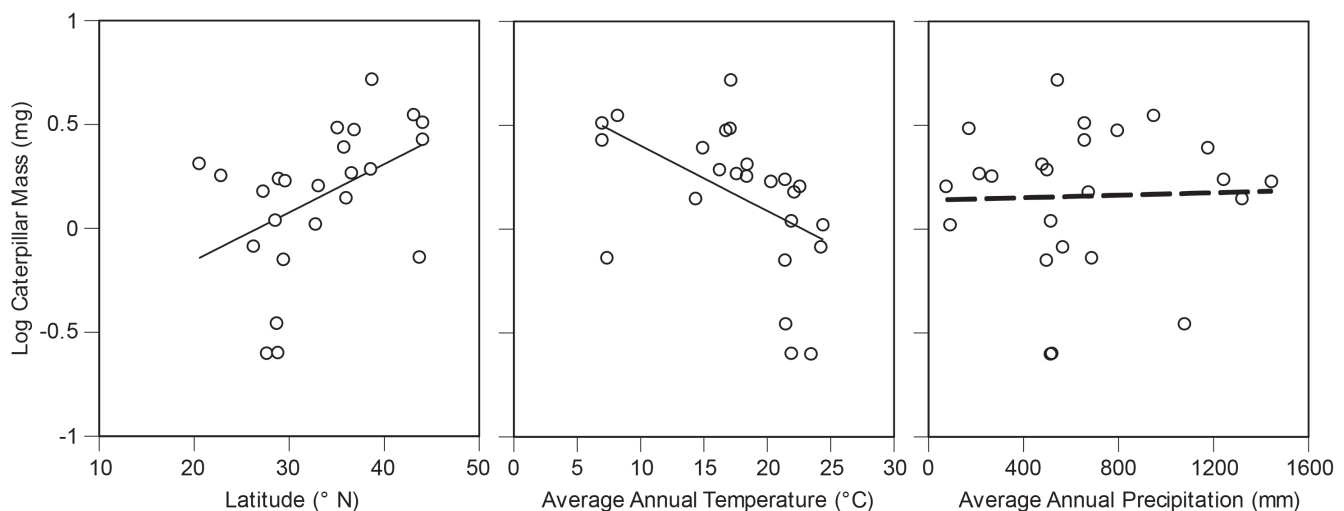


Figure 1 – The mass of *Helicoverpa zea* caterpillars fed the tissues of *Helianthus annuus* collected from different latitudes was positively related to the latitude of the collection site (A), negatively related to the average annual temperature of the collection site (B), indicating stronger herbivore defenses at lower latitudes and higher temperatures, but unrelated to average annual precipitation of the collection site (C). Solid line = significant relationship; dashed line = non-significant relationship).

was positively related to latitude ($r^2 = 0.1690$, model $F_{1,22} = 4.49$, $p = 0.0456$), mean log leaf length showed only a non-significant positive relationship with latitude ($r^2 = 0.1181$, model $F_{1,22} = 2.95$, $p = 0.1002$) and mean number of leaves exhibited no relationship to latitude ($r^2 = 0.0224$, $F_{1,22} = 0.51$, $p = 0.4848$). Though latitude and temperature were significantly negatively correlated, the relationship between the plant size measures and temperature differed slightly from the relationship between size and latitude. Mean log height was negatively, but not significantly, related to temperature ($r^2 = 0.1514$, model $F_{1,22} = 3.93$, $p = 0.0602$), but mean log leaf length ($r^2 = 0.0866$, model $F_{1,22} = 2.09$, $p = 0.1628$) and

mean log number of leaves ($r^2 = 0.0001$, $F_{1,22} = 0.00$, $p = 0.9763$) were unrelated. Plant size was also not related to average annual precipitation (mean log plant height ($r^2 = 0.0053$, model $F_{1,22} = 0.13$, $p = 0.7352$), mean log leaf length ($r^2 = 0.0414$, model $F_{1,22} = 0.95$, $p = 0.3403$) and mean number of leaves ($r^2 = 0.0166$, model $F_{1,22} = 0.37$, $p = 0.5481$)) or longitude (mean log plant height ($r^2 = 0.0725$, model $F_{1,22} = 1.72$, $p = 0.2032$), mean log leaf length ($r^2 = 0.0078$, model $F_{1,22} = 0.17$, $p = 0.6823$) and mean number of leaves ($r^2 = 0.0489$, model $F_{1,22} = 1.11$, $p = 0.3042$)).

A tradeoff between growth and herbivore resistance (represented by herbivore biomass gain) was indicated by signif-

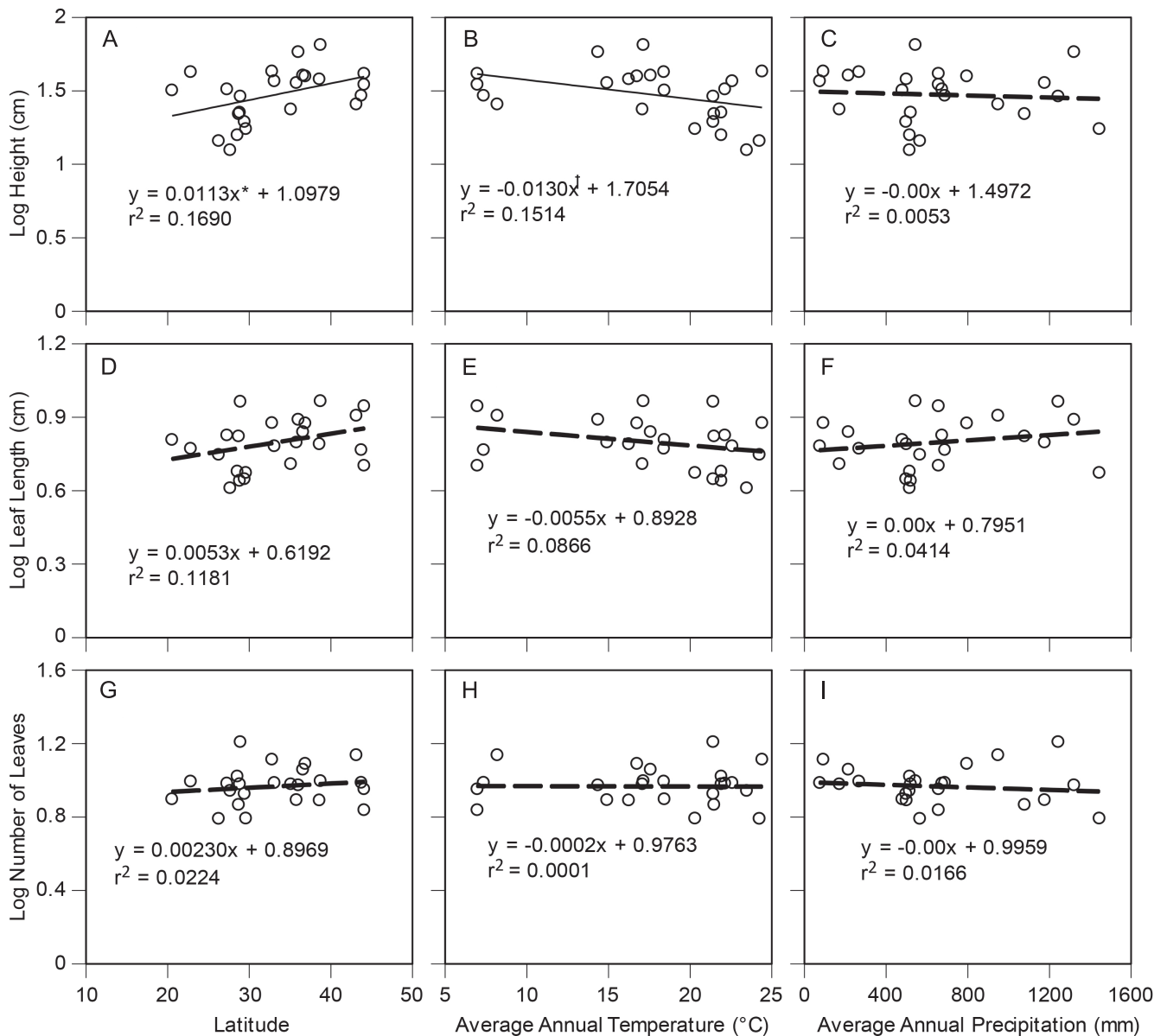


Figure 2 – Average height of *Helianthus annuus* after nine weeks was positively related to the latitude of the population from which the seeds were collected (A) and negatively related to the average annual temperature at the site (B), indicating more rapid growth at higher latitudes and lower average annual temperatures. Average leaf length was marginally positively related to latitude (D), but unrelated to average annual temperature (E). Average number of leaves was related to neither latitude nor average annual temperature (G and H). No measure of plant size was related to average annual precipitation at the collection site (C, F, I). (Solid line = significant relationship; dashed line = non-significant relationship).

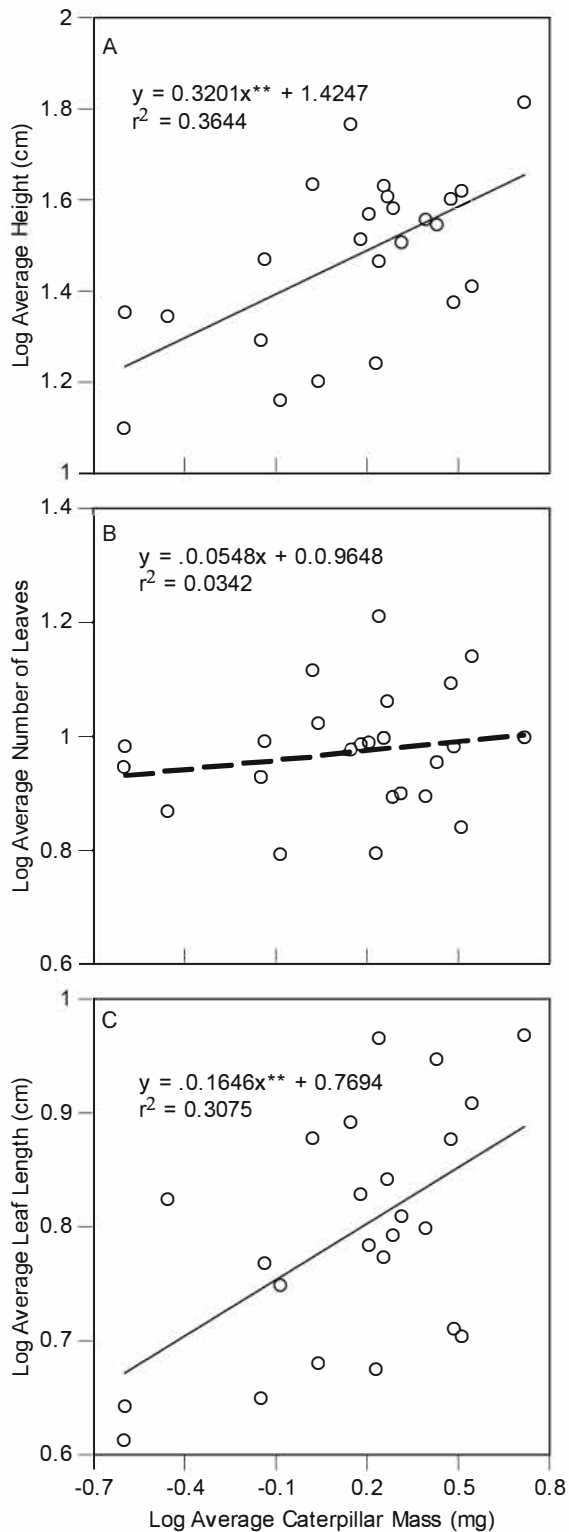


Figure 3 – Average height (A) and average leaf length (C) were positively related to the average mass of *Helicoverpa zea* caterpillars fed *Helianthus annuus* leaves collected from different latitudes, indicating a potential tradeoff between growth and herbivore resistance (indicated by caterpillar size, with smaller caterpillars associated with more resistant plants). Average number of leaves (B) was unrelated to caterpillar size. (Solid line = significant relationship; dashed line = non-significant relationship).

icant negative associations (as indicated by linear regression) between two of the three size variable means and mean caterpillar mass (mean log plant height ($r^2 = 0.3644$, model $F_{1,22} = 12.62$, $p = 0.0018$), mean log leaf length ($r^2 = 0.3075$, model $F_{1,22} = 9.77$, $p = 0.0049$)) (fig. 3). However, there was no relationship between the mean number of leaves and mean caterpillar mass ($r^2 = 0.0342$, $F_{1,22} = 0.78$, $p = 0.3872$).

DISCUSSION

A large body of literature supports the hypothesis that plant populations experience greater herbivory at lower latitudes (Garibaldi et al. 2011; Zhang et al. 2011; Więski & Pennings 2014; Heimonen et al. 2015; Lenhda & Ågren 2015) owing to longer growing seasons, higher levels of diversity in the herbivore community, and the stimulatory effect of high temperatures (Bezemer et al. 1998) on insect growth rates. Here, I have demonstrated that *H. annuus* populations from lower latitudes exhibit both increased resistance to herbivory and slower growth. Interestingly, neither resistance nor growth was related to average annual precipitation.

Temperature and latitude were equally good predictors of plant size after nine weeks (fig. 2). However, many variables beyond temperature are correlated with latitude (for example, length of the growing season, day length, diversity of the herbivore community, leaf nitrogen content, etc.), making it impossible to discern if temperature is the main factor influencing plant growth rates. In contrast, temperature explained 30% of the variation in herbivore resistance, while latitude accounted for only 20% of the variation, making temperature a slightly better predictor of herbivore resistance than latitude (fig. 1). Insects have been shown to respond more strongly to increased temperatures than most plant species, displaying faster growth and reproduction (Yang et al. 2007; Berg et al. 2010). The greater influence of temperature on herbivore resistance suggests that as climate warms and insect growth rates increase, plants that invest more resources in herbivore resistance may have a selective advantage and increase in frequency in the population.

Cold temperatures slow mineralization and decomposition rates, reducing the availability of nutrients and creating latitudinal gradients in the availability of both nitrogen and phosphorous. Based on experiments involving the application of chemical fertilizers, plants growing in more nutrient rich environments should produce more nutritive tissues (Awmack & Leather 2002; Uesugi 2015; Mendes & Cornelissen 2017). Yet, a meta-analysis of global nutrient patterns (Reich & Oleksyn 2003) demonstrated that the nitrogen and phosphorous content of the leaves of herbaceous plants declined with increasing mean annual temperature (and decreasing latitude). Several studies have demonstrated the adaptive potential of reducing the nutritive quality of leaves (to herbivores) on plant fitness. The slow-growth high-mortality hypothesis (SGMH) suggests that traits that slow the growth of insect herbivores increase the likelihood of those herbivores experiencing predation or parasitism by prolonging the most vulnerable, i.e., juvenile, stage of life (Moran & Hamilton 1980; Lundberg & Åström 1990; Uesugi 2015; Mendes & Cornelissen 2017). Although it is not clear if latitudinal trends in leaf nutrient content were the result of ad-

aptation or acclimation to the local climate and soil nutrient availability, the lower nutrient content may be a reflection of higher intensity of herbivory at lower latitudes.

In this study, it is not possible to distinguish the strategy employed by lower latitude plants to reduce herbivore damage and it is an interesting question for future research. However, this phenomenon further emphasizes the importance of relying on herbivore performance to assess plant resistance rather than attempting to predict which particular defensive trait (e.g., chemical compound, leaf toughness, etc.) constitute a plant's defenses. Insect growth rates reflect both a plant's investment in defense and the nutritive quality of its leaves. In addition to, or instead of, increased investment in resistance compounds, herbivory may select for plants that produce tissues of lower nutritional value. In fact, a meta-analysis conducted by Carmona et al. (2011) found no relationship between the production of secondary metabolites and a resistance to herbivory.

Growth is intricately linked to herbivore resistance (Dorrmann 2002; Kempel et al. 2011) and there is clear evidence of a tradeoff between growth and defense in *H. annuus*. Low latitude populations were not only better defended against herbivores, they also grew more slowly than high latitude plants. Resources dedicated to the production of defensive compounds cannot be used for growth. As a result, plants with poor resistance to herbivory are expected to grow more quickly than those investing heavily in defensive compounds (de Jong 1995; Van der Putten et al. 2010). As this investment in herbivore resistance comes at the cost of investment in size (fig. 3), the predicted change in global temperatures could alter biotic interactions and plant productivity.

Ecosystem productivity is a product of both temperature and precipitation. It is surprising, then, that plant growth rates were unrelated to the average level of precipitation at seed collection sites. A study of drought adaptation in *Lasthenia californica* DC. ex Lindl. also did not show an adaptive response to drought when growth alone was considered but, was found in relation to reproductive success, i.e., flower production (Rajakaruna et al. 2003). Adaptations to different precipitation levels may only be apparent when moisture availability (in the form of droughts or floods) causes stress. Average cumulative precipitation levels at all collection sites may be sufficient to prevent any drought stress, removing any selection pressures. It is possible that correlations between growth rates and average cumulative precipitation may only be visible when precipitation levels are below a particular threshold. Above the threshold, water availability may not affect growth.

Alternatively, in this study, adaptations to low water availability (i.e., drought tolerance) may not have been observable as the sunflowers did not experience any drought stress. Plants adapted to arid environments maximize growth when water is available (Pereira et al. 2007). If this is the case, it would suggest that there are no costs to drought tolerance. Many ecotypes adapted to environmental stressors, e.g., salt, heavy metals, etc., exhibit slower growth in benign environments.

Many studies predict higher levels of herbivory in lower latitude communities. Though measurements of actual herbi-

vore damage have provided conflicting results with studies demonstrating both elevated and reduced herbivory at low latitudes, examination of plant adaptations to the environment have clearly demonstrated an evolutionary response to elevated herbivory at lower latitudes (Salgado & Pennings 2005). Examinations of latitudinal gradients in plant-herbivore interactions may enhance predictions of how communities are likely to change in response to a warmer climate. *Helianthus annuus* exhibited both increased resistance to herbivores and slower growth at lower latitudes and higher temperatures, suggesting that as the climate warms and populations of insect herbivores increase in abundance, plant growth in northern latitudes may be slowed as plants begin to invest more resources in resistance. Herbivore defenses were unrelated to precipitation, suggesting that temperature changes will drive biotic interactions to a greater extent than changes in rainfall patterns.

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